

**Genetic Factors Governing Resistance and
Susceptibility of Oats to *Puccinia coronata*
Corda var. *avenae*, F. and L., Race 57**

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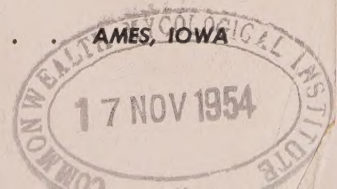
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RESEARCH BULLETIN 411 JULY, 1954

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SUMMARY

Corrected F_2 data from 23 oat crosses involving eight major sources of resistance to crown rust were used to determine the inheritance of resistance and susceptibility to crown rust race 57.

The varieties used as parents and their assigned factors for resistance or susceptibility, other than recessive alleles, to race 57 were as follows:

1. Klein 69B—Resistant—KK
2. Landhafer—Resistant—LL
3. Victoria—Resistant—VV
4. Santa Fe—Resistant— M_1M_1 or $M_1M_1 U_1\dot{U}_1$
5. Ukraine—Resistant—MM UU
6. Trispermia—Resistant— M_2M_2 and/or two other factors
7. Anthony-Bond x Boone—Resistant— $M_2M_2 V_1V_1$ and sometimes one other factor
8. Clinton—Susceptible— I_kI_k

The allelic and non-allelic relationships with regard to dominance and/or epistasis were in the following order:

MM or UU > M_1M_1 or U_1U_1 or LL > VV > M_2M_2 or U_1U_1 or I_kI_k > KK

The genes designated as M and U were linked with $22.88 \pm .04$ percent recombination.

Genetic Factors Governing Resistance and Susceptibility of Oats to *Puccinia coronata* Corda var. *avenae*, F. and L., Race 57¹

By VERNE C. FINKNER²

Many oat investigators believe that disease-resistant varieties can be maintained only by continuous breeding to keep pace with the uncontrollable change in races of highly specialized obligate parasites such as *Puccinia coronata avenae*, which causes crown rust of oats. This concept is being utilized at the present time in oat breeding programs by supplementing the Bond type of crown rust resistance with other types of resistance to prevalent races which now attack Bond and its derivatives. If these methods continue to be the hope of maintaining disease resistance, the efficiency of the program depends upon the rapid transfer of genes for crown resistance to agronomically desirable varieties. The most satisfactory method to attain this efficiency would be to catalog genetic factors and combinations of genetic factors for resistance to specific races. Such information would facilitate rapid transfer of resistance to agronomically desirable varieties for any race of rust which appears as a potential threat to present-day varieties.

The literature on inheritance of resistance to crown rust is summarized in table 1. The process of cataloging is complicated due to the large number of races of the crown rust fungus, the method by which they are identified and the number of sources of resistance. The allelic relationship of the factors for resistance shown in table 1 are not all known. Cochran, *et al.* (1), Litzenberger (6) and Weetman (11) have shown the Victoria factor pair and the Bond factor pairs to be independent. Litzenberger (6) has shown that the two Bond factor pairs are independent of the Santa Fe factor pair and that Santa Fe carries one of the complementary Bond factors. Weetman (11) assumed the complementary factor pairs of Ukraine were allelic to the Bond factors.

The process of cataloging is further complicated by the fact that it is not known how many race reactions are controlled by each factor, nor the interaction that may occur if more than one

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TABLE 1. TABULAR SUMMARY OF GENETIC INTERPRETATIONS GOVERNING RESISTANCE OR SUSCEPTIBILITY TO *Puccinia coronata avenae*, RACES USED, SOURCE OF RESISTANCE, AND REFERENCES.

Source	Races	Genetic interpretation of factors governing resistance	Reference
Victoria	1, 45	Single factor pair.	1, 6, 8, 11
Santa Fe	1, 45	Single factor pair.	6
	45	Single factor pair and two complementary factor pairs.	9
	1	Single factor pair and one of two complementary factor pairs.	6
Landhafer	1, 3, 4, 5, 6, 33, 57, 68	Single factor pair.	4, 6
Ukraine	Biotype of race 1	Two complementary factor pairs.	11
Sunrise 23	33	Single factor pair.	2
Red Rustproof	33	Single factor pair.	2
Algerian-Calcutta	33	Single factor pair.	2
Bond	3, 6, 1	Two complementary factor pairs.	1, 3, 5, 11
Fulghum	33	Inhibitor factor pair to Sunrise 23 type of resistance.	2
Iowa 444	1, 7, 46	Inhibitor factor pair to Bond type resistance.	10
Richland-Fulghum	1	Two complementary inhibitor factor pairs to Bond type resistance.	1

factor pair for resistance is used. The results from this investigation answer some of these questions for one race of the crown rust organism.

MATERIALS AND METHODS

The parental varieties used in this study were furnished by Dr. H. C. Murphy of the USDA, and were as follows: (1) Klein 69B, C.I. 4118; (2) Trispermia, C.I. 4009; (3) Victoria, C.I. 2401; (4) Santa Fe, C.I. 4518; (5) Ukraine (sometimes called Mutica or Mutica Ukraine), C.I. 3259; (6) Landhafer, C.I. 3522; (7) Clinton, C.I. 5011; and (8) Anthony-Bond x Boone, C.I. 5220.

Of the possible 28 crosses among these varieties, disregarding reciprocals, 23 were obtained and the actual parents involved in each cross were maintained as individual lines.

The F_1 plants were tested for reaction to a mixture of races of crown rust which parasitize Clinton (predominantly races 45 and 57). Approximately 100 F_2 plant progenies from one F_1 plant of each of the 23 crosses were classified according to

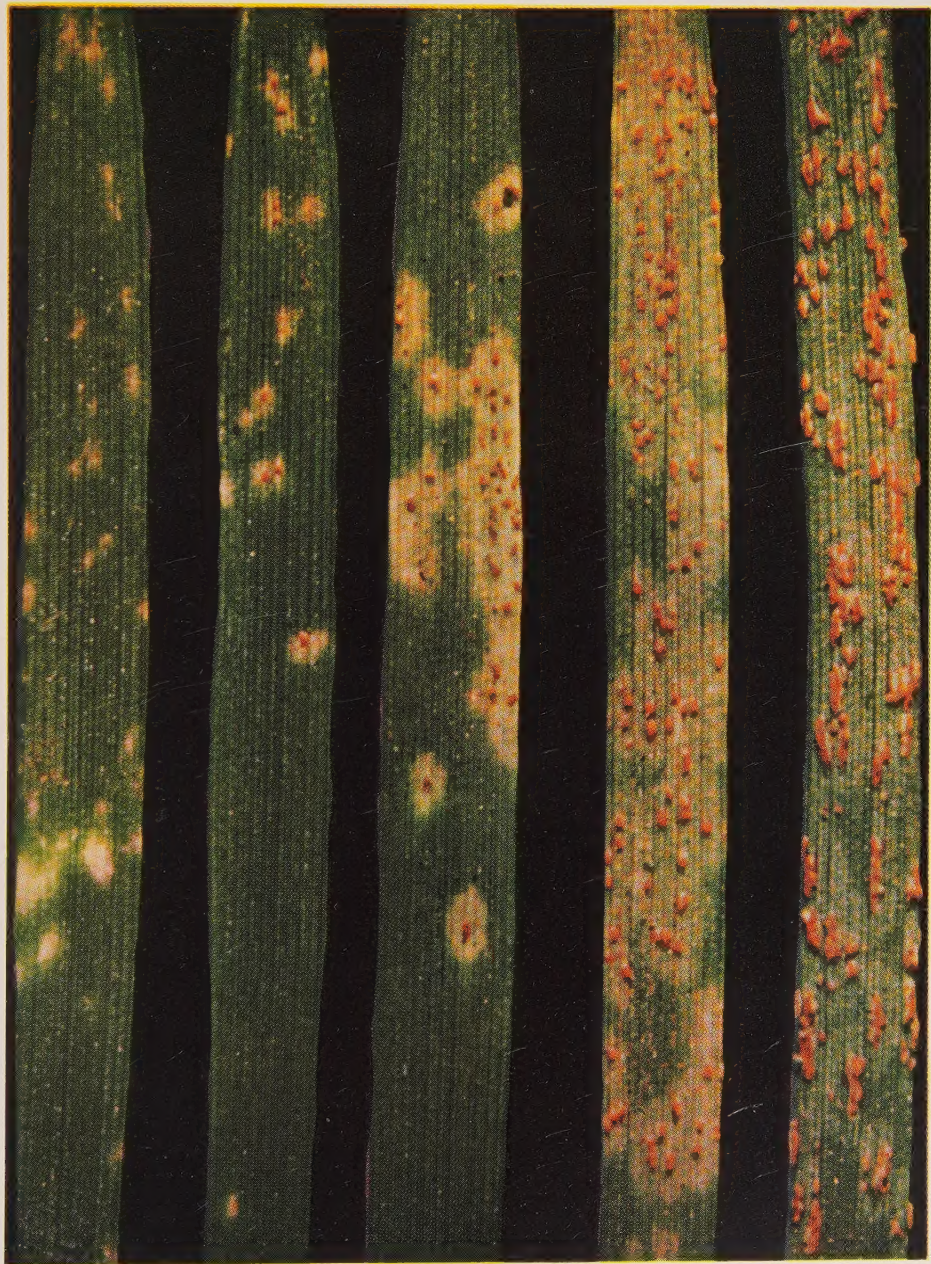


Fig. 1. Infection types of crown rust. Left to right: "0" type of pronounced necrotic flecks or lesions; "1" type of minute uredia surrounded by solid necrotic areas; "2" type of small uredia with hypersensitive areas varying from sharp necrosis to pronounced chlorosis; "3" type of medium size uredia with chlorosis but no necrosis and usually considered susceptible; "4" type of large confluent uredia and considered as fully susceptible.

The immune "I" type is shown in fig. 4, Victoria "V" type in fig. 3, and the mesothetic "X" type in fig. 2.



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their phenotypic crown rust reaction to race 57. These F_2 plants were further classified genotypically by a progeny test in F_3 to the same race of crown rust. The average number of progenies from each F_2 plant was smaller than desired, being only about 12 plants.

All crown rust reactions were obtained under greenhouse conditions in the first leaf stage. Inoculations of F_1 and F_2 plants were made by (1) removing bloom from leaf by gently rubbing leaf with moistened fingers, (2) placing crown rust spores on leaf with a scalpel, (3) placing plants in a humidity chamber, atomizing with water and leaving in a chamber for approximately 16 hours. Seedling reactions were recorded 12 to 14 days after inoculation.

Inoculation of the F_3 seedlings was made by dusting seedlings with a talcum-crown rust mixture. Procedure following inoculation was the same as used for the F_2 . Parental types were included as checks.

Crown rust reaction was recorded for each individual seedling whenever practicable. The crown rust reaction types used for classification were as described by Murphy (7). Figure 1 shows the typical crown rust reaction types used.

EXPERIMENTAL RESULTS

PARENTS AND F_1 CROSSES

Photographs of the crown rust reaction of the parent varieties to race 57 are shown in figs. 2, 3, 4 and 5. The variety Klein 69B was inconsistent and mesothetic in its reaction to race 57 in the greenhouse. Pustules generally were surrounded by a necrotic area or by a green area which in turn was surrounded by a necrotic area (green island effect).

The variety *Trispermia* showed varying degrees of resistance to race 57, indicating that this variety may be a mixture of genotypes. The average reading given this variety was a "2" type.

The varieties *Victoria*, *Santa Fe* and *Landhafer* were resistant to race 57 in the greenhouse. *Victoria* had a characteristic reaction which differed from that of any of the other varieties. *Santa Fe* and *Landhafer* had a "0" type reaction to race 57.

The variety *Ukraine* was immune to this collection of crown rust race 57 although it has been reported to be susceptible to biotypes of this race.

The selection *Anthony-Bond* x *Boone* bordered between a resistant and a susceptible reaction. Since it was clearly not fully susceptible to race 57, it was classified as resistant.

The variety *Clinton* was fully susceptible to race 57.

From observations of several thousand rust-infected plants in the greenhouse it was noted that changes in the environmental conditions would alter the rust reaction type. This change in

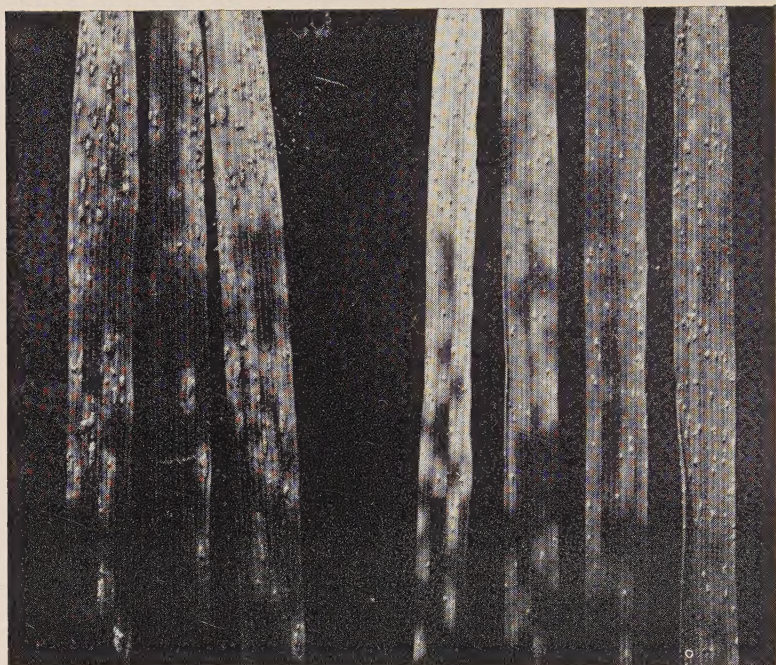


Fig. 2. Rust reaction of the parental varieties Klein 69B and Trispemia. Left to right. Left half: three leaves from Klein 69B. Mesothetic type reaction. Right half: four leaves from Trispemia. Variable reaction of the "2" type.

reaction was usually not great and only in the borderline cases did it cause difficulties. Environmental conditions less favorable for plant growth changed rust reaction toward an intermediate type, i.e., highly resistant plants were less resistant and highly susceptible plants less susceptible. As will be noted later, the field and greenhouse reactions of the parents did not agree in all cases, but plants never were more susceptible in the field than in the greenhouse.

In most cases the F_1 reaction was intermediate to the parental reactions.

CROSSES BETWEEN RESISTANT AND SUSCEPTIBLE PARENTS

Crosses between resistant and susceptible varieties were expected to give information on number of factor pairs and type of gene action determining resistance and susceptibility to a specific race of the crown rust organism.

RESISTANCE CONTROLLED BY A SINGLE FACTOR PAIR

From crosses involving susceptible Clinton with resistant Landhafer, Santa Fe and Victoria, the corrected F_2 data³ presented

³ F_2 genotype based on breeding behavior in F_3 .

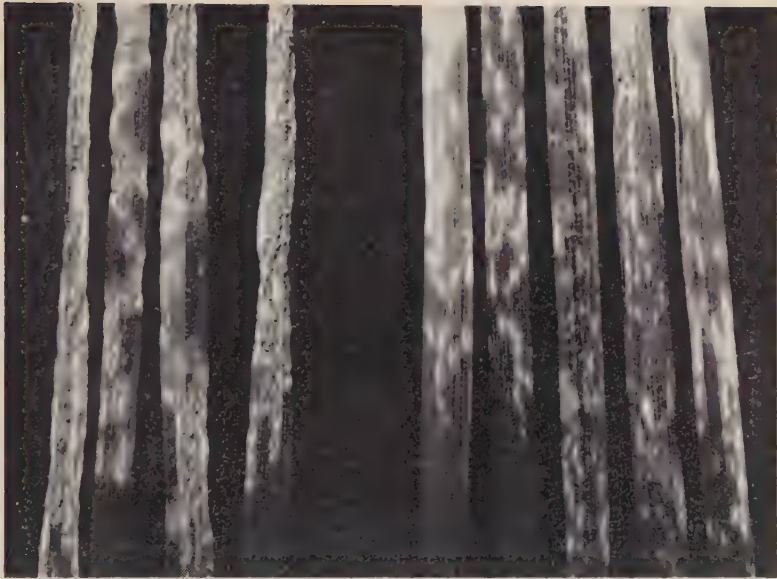


Fig. 3. Rust reaction of the parental varieties Victoria and Santa Fe. Left to right. Left half: four leaves from Victoria showing typical Victoria reaction. Right half: five leaves from Santa Fe showing "0" to "1" type reaction.

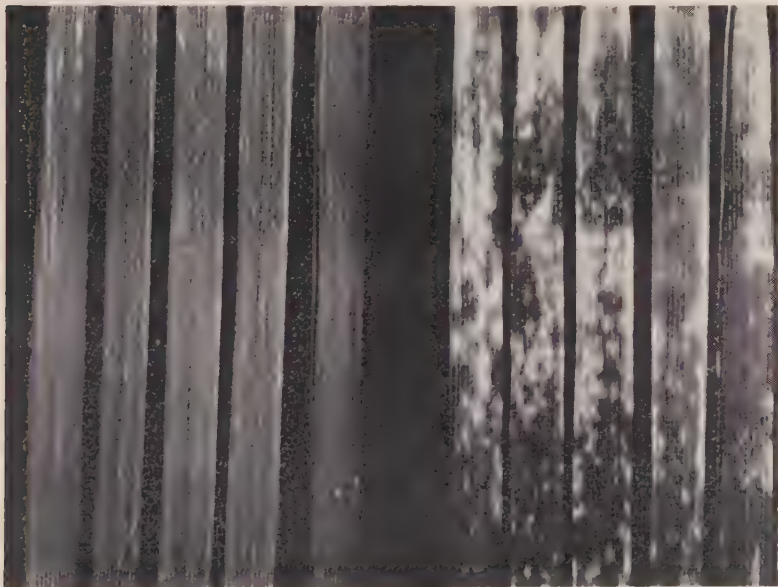


Fig. 4. Rust reaction of the parental varieties Ukraine and Landhafer. Left to right. Left half: five leaves from Ukraine showing "1" reaction. Right half: five leaves from Landhafer showing "0" reaction.



Fig. 5. Rust reaction of the parental varieties Clinton and Anthony-Bond x Boone. Left to right, Left half: five leaves from Clinton showing "4" type reaction. Right half: four leaves from Anthony-Bond x Boone showing variable reaction of this variety.

in table 2 indicated that resistance was controlled by a single factor pair. Since the reaction of each plant was recorded individually in F_3 , an additional test of the proposed genetic ratio was obtained from the segregating portion of the population. This test was based on phenotypic classification but usually involved a much larger population. The observed data are shown in table 3.

As shown in table 2 the corrected F_2 data are in agreement with the hypothesis in the crosses of Clinton with Landhafer and Victoria, while a poor fit was obtained in the cross of Santa Fe x Clinton. A satisfactory fit was obtained if the plants breed-

TABLE 2. OBSERVED AND EXPECTED FREQUENCIES OF GENOTYPIC CLASSES FOR A 1:2:1 RATIO FOR REACTION TO RACE 57 CROWN RUST BASED ON CORRECTED F_2 DATA FOR CROSSES BETWEEN SUSCEPTIBLE CLINTON WITH RESISTANT LANDHAFAER, SANTA FE AND VICTORIA.

Cross	Genotype						Chi-square	Probability
	Resistant Obs.	Exp.	Segregating Obs.	Exp.	Susceptible Obs.	Exp.		
Landhafer x Clinton	14	18	38	36	20	18	1.2	0.7-0.5
Santa Fe x Clinton	43	29	47	58	26	29	9.2	<0.01
Clinton x Victoria	34	31	64	63	27	31	0.9	0.5-0.3

TABLE 3. OBSERVED AND EXPECTED FREQUENCIES OF PHENOTYPIC CLASSES FOR A 3:1 RATIO FOR REACTION TO RACE 57 CROWN RUST FOR SEGREGATING F_2 LINES OF CROSSES OF SUSCEPTIBLE CLINTON WITH RESISTANT LANDHAFFER, SANTA FE AND VICTORIA.

Cross	Resistant		Susceptible		Chi-square	Probability
	Obs.	Exp.	Obs.	Exp.		
Landhafer x Clinton	313	353	158	118	14.7	<.01
Santa Fe x Clinton	748	704	190	234	11.0	<.01
Clinton x Victoria	979	1023	385	341	7.6	<.01

ing true resistant or segregating were grouped together. The expected numbers then were 87 resistant to 29 susceptible and the observed 90 to 26. The poor fit for this cross probably was due to an insufficient number of progenies tested to separate the true breeding resistant and the segregating genotypes.

The poor agreement between the observed and expected numbers in table 3 cannot be satisfactorily explained.

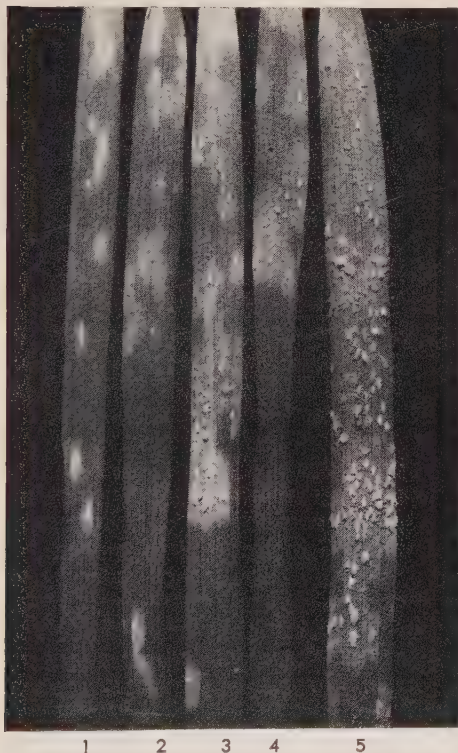


Fig. 6. Typical segregation obtained in the F_2 from crosses of resistant Santa Fe by susceptible Clinton where resistance was controlled by a single factor pair. Left to right: (1-2) resistant parental types, (3-4) intermediate types; (5) fully susceptible parental type.

The typical F_2 segregation obtained in these crosses is shown in fig. 6.

RESISTANCE CONTROLLED BY OTHER THAN A SINGLE FACTOR PAIR

Progenies of crosses of susceptible Clinton with resistant Klein 69B, Trispermia, Ukraine, and Anthony-Bond x Boone indicated that more than a single factor pair controlled the resistance of these varieties. The observed and expected frequencies of genotypic classes for reaction to race 57 based on corrected F_2 data are given in table 4. Since the gene action varied in most of these crosses, they will be discussed separately.

The data from the cross Klein 69 x Clinton suggested the presence of a dominant inhibitor factor from Clinton which was epistatic

TABLE 4. OBSERVED AND EXPECTED FREQUENCIES OF GENOTYPIC CLASSES FOR REACTION TO RACE 57 CROWN RUST BASED ON CORRECTED F_2 DATA FOR CROSSES OF SUSCEPTIBLE CLINTON WITH RESISTANT KLEIN 69B, TRISPERNIA, ANTHONY-BOND x BOONE, AND UKRAINE.

Cross	Resistant		Genotype Segregating		Susceptible		Chi-square	Probability
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.		
Klein 69B x Clinton*	51	49	55	57	7	7	0.3	0.9
Trispernia x Clinton†	87	86	56	60	5	2	4.8	0.1
Clinton x (Anthony-Bond x Boone)‡	62	54	56	62	6	8	2.3	0.3
Ukraine x Clinton§	50	49	67	69	21	20	0.0	0.9

*Single factor pair from Klein 69B determining resistance. Single factor pair from Clinton which inhibits the Klein 69B factor.

†Three independent factor pairs for resistance from Trispernia.

‡Two independent factor pairs for resistance from Anthony-Bond x Boone.

§Two linked factor pairs for resistance from Ukraine with 23 percent crossing over.

to the dominant factor pair for resistance from Klein 69B. The corrected F_2 data agreed very well with the hypothesis, as shown in table 4. The observed phenotypic ratio of resistant and susceptible F_3 plants from the segregating portion of the population did not agree with the expected. Three different genotypes were expected to segregate in the F_3 . The portion with the assumed genotype homozygous recessive for the inhibitor factor and heterozygous for the resistance factor was expected to segregate 3 resistant to 1 susceptible. The observed numbers were 167 resistant to 47 susceptible where 160 to 54 were expected. This was a satisfactory fit. In the classes where the inhibitor factor was assumed heterozygous, major discrepancies were found. This probably was due to the incomplete epistasis of the heterozygous inhibitor factor over the factor for resistance. When these two heterozygous classes were grouped, the expected numbers were 107 resistant to 409 susceptible while the observed numbers were 139 resistant to 377 susceptible.

In the cross of Trispernia x Clinton the corrected F_2 data indicated that three factor pairs conditioned the resistant reaction of Trispernia, each factor pair capable of producing a resistant reaction. The agreement between the observed and expected numbers as shown in table 3 was satisfactory. Reactions of individual F_3 seedlings were not recorded in this cross because partial dominance made the phenotypic classification unreliable.

From the corrected F_2 data on 124 plants from the cross Clinton x (Anthony-Bond x Boone) the observed numbers as shown in table 4 indicated two independent factor pairs, each partially dominant and capable of producing a resistant reaction, governing the resistant reaction of Anthony-Bond x Boone. The expected numbers were 54 to breed true resistant, 62 to segregate resistant and susceptible and 8 to breed true susceptible. The observed numbers were 62, 56 and 6. This is a satisfactory agreement of the observed with the expected.

In the segregating portion of the population the observed F_3 numbers were 775 resistant to 169 susceptible, and the expected were 850 to 94. Partial dominance may have accounted for the phenotypic misclassification.

The cross Ukraine x Clinton involved the extremes in crown rust reaction types, Ukraine being immune from and Clinton fully susceptible to the biotype of race 57 used in this study. On the basis of the F_2 data, corrected by progeny tests, the following segregation was obtained: 50 bred true for Ukraine type of resistance, 67 segregated into parental types and 21 bred true for susceptibility. It was evident that an assumption of independent inheritance could not explain these data.

By assuming that Ukraine carried two linked factor pairs for resistance, each being dominant, and each capable of producing the Ukraine type of resistance, the linkage was estimated from the corrected F_2 data. It should be pointed out that all crossover types could not be distinguished from the non-crossover types even by the progeny test. The best linkage estimate could be made on the basis of the three identifiable corrected F_2 classes, i.e., breeding true for parental types and segregating for parental types.

The estimation of linkage intensity was made by using the maximum likelihood method. This estimate was 23 percent crossing over, or the gametic frequency of each parental gamete was 38.5 percent and that of each crossover gamete was 11.5 percent.

The process of linkage estimation used one degree of freedom leaving one to test goodness of fit. Where the expected numbers were 49 resistant, 69 segregating and 20 susceptible, the observed numbers were 50, 67 and 21, respectively. This obviously is a good fit as shown in table 4. A more critical test of the hypothesis in this cross was obtained from the comparison of observed and expected numbers of F_3 resistant and susceptible plants in the segregating portion of the population. These data were not used in the estimation of linkage, but only two phenotypic classes could be recognized with certainty.

In the progenies from the segregating portion of the F_2 population it was expected that 64.8 percent would be double heterozygotes. Of these, 91.4 percent were expected to be in the coupling phase and segregate 85.2 percent resistant and 14.8 percent susceptible. The 8.6 percent in the repulsion phase were expected to segregate 98.7 percent resistant and 1.3 percent susceptible. The segregation of this class was therefore expected to be 86.3 percent resistant and 13.6 percent susceptible.

In the other two segregating genotypes (35.2 percent) the segregation was expected to be 75 percent resistant and 25 percent susceptible. The total segregation therefore was expected

to be 82.3 percent resistant and 17.7 percent susceptible. The expected numbers were 1,529 to 329 and the observed 1,542 to 316. This was a satisfactory agreement with the hypothesis.

CROSSES AMONG RESISTANT PARENTS

In the previous section a genotype was proposed for each of the crown rust resistant parents based on the ratios obtained from crosses with a fully susceptible parent. Data from crosses among the resistant varieties should provide supporting evidence for the proposed genotypes of the parents and should give data on the extent to which certain of the genes for resistance are allelomorphous. Critical data from crosses among resistant varieties are the occurrence of homozygous susceptible progenies and progenies segregating for resistance and susceptibility. These segregates clearly indicate either that the parents had non-allelic genes for resistance to crown rust or that there might be factors present which complemented each other to cause susceptibility. There also was some possibility that complementary factors were causing susceptibility since the F_1 plants showed some degree of resistance.

The absence of susceptible plants in the progeny from a cross between two resistant varieties indicated that the factors governing resistance were allelomorphous or very closely linked. In many cases the types of resistance of the parents were sufficiently different to classify the segregates into parental types.

RESISTANT VARIETIES HAVING ALLELOMORPHIC GENES FOR RESISTANCE TO CROWN RUST RACE 57

From the cross Ukraine x Trispermia no susceptible plants were observed in either the F_2 or F_3 generations. Therefore, Trispermia carried at least one factor pair for resistance allelic to one of the duplicate linked factor pairs from Ukraine.

Assuming the Ukraine factors (immune reaction) were epistatic and/or dominant to the Trispermia factors (2 type), the expected corrected F_2 ratio as shown in table 5 was the same as for the cross Ukraine x Clinton. The observed numbers were 44 breeding true Ukraine type, 55 segregating Ukraine and Trispermia, and 17 breeding true Trispermia, while the expected numbers were 41 to 58 to 17. This was a satisfactory fit.

On the basis of the segregating portion of the population a ratio of 82.3 percent Ukraine and 17.7 percent Trispermia types was expected; or from a total of 860 F_3 plants the expected was 708 to 152 and the observed was 677 to 183. A Chi-square value of 7.7 was obtained with a probability of less than 0.1.

In the cross Ukraine x Santa Fe no susceptible plants were observed in the F_2 or F_3 generations indicating that the Santa Fe factor pair was allelic to one of the linked Ukraine factor pairs. Since the Ukraine factors were dominant and epistatic

TABLE 5. OBSERVED AND EXPECTED FREQUENCIES OF GENOTYPIC CLASSES FOR REACTION TO RACE 57 CROWN RUST BASED ON CORRECTED F₂ DATA FOR CROSSES BETWEEN RESISTANT PARENTS HAVING ALLELOMORPHIC FACTORS FOR RESISTANCE.

Cross*	Genotype						Chi-square	Probability
	Female type		Segregating		Male type			
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.		
Ukraine x Trispermia†	44	41	55	58	17	17	0.38	0.8-0.9
Ukraine x Santa Fe†	52	52	70	74	26	22	0.95	0.5-0.7
Ukraine x (A.B.xBoone)	17	22	36	32	10	9	1.75	0.3-0.5
Trispermia x Santa Fe‡	8	13	47	46	36	32	2.44	0.2-0.3
Santa Fe x (A.B.xBoone)‡	42	35	64	70	34	35	1.94	0.3-0.5
Victoria x (A.B.xBoone)§	30	26	46	53	29	26	1.89	0.3-0.5

*Female parent listed first in each cross.

†Two linked factor pairs for Ukraine type reaction with 23 percent crossing over were dominant and epistatic to the Trispermia and Santa Fe type of resistance.

‡Santa Fe type of resistance was dominant and epistatic to the Trispermia and Anthony-Bond x Boone type of reaction.

§Victoria type of resistance was dominant and epistatic to the Anthony-Bond x Boone type of resistance.

to the Santa Fe factor, the expected ratios were the same as in the previous cross. The observed numbers were 52 breeding true Ukraine (immune), 70 segregating Ukraine and Santa Fe types, and 26 breeding true Santa Fe (0 type), and the expected numbers were 52 to 74 to 22. This was a satisfactory fit as indicated in table 5.

In the segregating portion of the population, accurate phenotypic classifications could not be made since the Ukraine type was only partially dominant or epistatic to the Santa Fe type. The use of talc-spore mixtures also tended to mask the rust reaction.

In the cross Ukraine x (Anthony-Bond x Boone) no susceptible plants were observed in the F₂ or F₃ generations. At least one factor for the Anthony-Bond x Boone type of resistance (2 type) therefore was allelomorphic to one of the factor pairs from Ukraine. The gene action again was partial dominance and epistasis of the linked Ukraine factors.

The expected ratio of corrected F₂ genotypes again was the same as in the previous two crosses. From a total of 63 plants the expected numbers were 22 breeding true Ukraine, 32 segregating Ukraine and (Anthony-Bond x Boone) and 9 breeding true Anthony-Bond x Boone type. The observed numbers of 17 to 36 to 10, as shown in table 5, were a satisfactory fit to the expected.

In the segregating portion of the population the expected phenotypic ratio again was 82.2 percent Ukraine and 17.7 Anthony-Bond x Boone type. From a total of 496 F₃ plants the expected numbers were 408 to 87 and the observed 389 to 107. A Chi-square value of 5.3 was obtained with a probability between 0.05 and 0.02.

The crosses of Ukraine with Klein 69B and Victoria resulted

in progenies which were fully susceptible, indicating that the factors governing resistance of these varieties were not allelomorph. The cross of Ukraine x Landhafer was not available for study.

Since Santa Fe had a single factor pair governing its resistance, crosses with Trispermia and Anthony-Bond x Boone should indicate if there was an allelomorph series involving one factor pair from Ukraine (immune), the factor pair from Santa Fe (0 type), and one of the factor pairs from Trispermia and Anthony-Bond x Boone (2 type). Both of these crosses were studied, and the corrected F_2 data are shown in table 5. As no susceptible plants were observed in the F_2 and only a few plants were classified as susceptible in the F_3 , it was assumed that Ukraine, Santa Fe, Trispermia and Anthony-Bond x Boone had at least one allelic factor pair for resistance.

The data from the cross Trispermia x Santa Fe did not fit the expected F_2 ratio of 1 Trispermia type to 2 intermediate to 1 Santa Fe type resistance. The data indicated that Santa Fe carried alleles to both Ukraine factors. The observed data agreed well with the expected under this hypothesis as shown in table 5, but not in the segregating portion in the F_3 . The expected ratios in F_3 were computed on the basis of complete dominance or epistasis of the Santa Fe factors over the Trispermia factors. This probably was not the case since partial dominance or epistasis was the rule in most crosses. All plants that showed any pustule formation were classified like the Trispermia type when probably some of these were heterozygotes.

The cross Santa Fe x (Anthony-Bond x Boone) involved a different Santa Fe parent from the one previously discussed, and the corrected F_2 fit a 1 to 2 to 1 ratio as shown in table 5. The segregating portion of the F_3 could not be satisfactorily classified because of incomplete dominance and epistasis.

The only other cross studied which did not give susceptible plants in the F_2 and F_3 was Victoria x (Anthony-Bond x Boone). The corrected F_2 data fit a 1 to 2 to 1 hypothesis as shown in table 5. The observed numbers in the segregating portion of the population were 442 Victoria type to 125 Anthony-Bond x Boone type, which agreed with the expected numbers 425 to 142.

The crosses of Victoria with Santa Fe and Trispermia were not available for study; however, since the Santa Fe type of resistance conditioned by a single factor pair was allelic with one of the two linked factor pairs of Ukraine and the Victoria factor was independent of the Ukraine factors, as will be shown later, it may be concluded that the Santa Fe factor and the Victoria factor are non-allelic. The data do not substantiate a definite conclusion as to whether or not the variety Trispermia has one of its three factor pairs allelic to the Victoria factor.

Fig 7. Typical segregation obtained in the F_2 of crosses of resistant by resistant parents where resistance was controlled by at least one allelomorphous factor pair. Left to right: (1) Ukraine parent, (2) recovery of Ukraine parental type, (3) reaction intermediate to either parent, (4) recovery of Anthony-Bond x Boone parental type, (5) Anthony-Bond x Boone parent.



Figure 7 shows the typical F_2 segregation of a cross between two resistant varieties whose resistance is controlled by allelic factors.

RESISTANT VARIETIES HAVING NON-ALLOMORPHIC GENES FOR RESISTANCE TO CROWN RUST RACE 57

In the crosses of Ukraine x Klein 69B, Ukraine x Victoria, Santa Fe x Landhafer, Victoria x Klein 69B, Victoria x Landhafer, Klein 69B x Landhafer, Trispermia x Landhafer, Santa Fe x Klein 69B and Klein 69B x Trispermia, susceptible plants were obtained in the F_2 and F_3 showing that the factors for resistance in the parental plants were non-allelic. These data supplemented the information on the number of factor pairs governing parental resistance.

These crosses were possibly the most interesting and important since they gave information concerning the possibility and advisability of combining factors for resistance from different parental sources.

1. *Crosses with the Victoria factor*

The corrected F_2 data from crosses of Ukraine, Klein 69B and Landhafer with Victoria are given in table 6. The occurrence of true-breeding susceptible F_3 lines shows that Ukraine, Klein 69B and Landhafer carry factors for resistance which are non-allelic to the Victoria factors for resistance. Additional information concerning the number of factor pairs involved and the degree of epistasis of type reactions also was obtained. For these purposes the crosses will be discussed separately.

In the cross Ukraine x Victoria it was assumed the two linked factors from Ukraine were epistatic to and independent of the single factor from Victoria. As shown in table 6, seven phenotypic classes could be recognized in the F_3 lines under such an assumption. The observed data fit the expected very well in all classes except the one breeding true for the Victoria type resistance where too many true-breeding lines occur. The discrepancy in this one class gives a high Chi-square value with a very low probability of occurring due to chance alone. A reason for this discrepancy is not apparent. A possible explanation is incomplete epistasis of a single Ukraine factor in the heterozygous condition. Since Ukraine had an immune type reaction, any pustule formation was classified as the Victoria type reaction.

In the portion of the population segregating for the parental types, a total of 143 F_3 plants was observed. Of these, 96 were classified as the Ukraine type and 47 as the Victoria type where the expected numbers were 119 to 24. Again too many plants were classified as having the Victoria type reaction. Discrepancies also were found in the class segregating for parental types and susceptibility. The observed numbers were 79 Ukraine to 35 Victoria to 17 susceptible where the expected numbers were 107 to 18 to 6. In the portion segregating for the Ukraine type resistance and for susceptibility the observed numbers were 62 to 27 where the expected numbers were 74 to 15. In the portion segregating for the Victoria type resistance and for susceptibility the observed numbers were 81 to 24 and the expected were 79 to 26.

In the cross Victoria x Klein 69B the assumed mode of inheritance was through a single independent factor pair from each parent. The corrected F_2 data are shown in table 6, but they do not give a satisfactory fit to the expected as measured by the Chi-square test. The Victoria factor was found to be epistatic to the Klein 69B factor; therefore the Victoria factor was expected to be recovered either in the homozygous or heterozygous condition in 75 percent of the F_3 lines. From the total of 78 lines it was recovered in 59 and not recovered in 19 lines, which agreed exactly with the expected. It was apparent then that the progeny tests were not of sufficient size to adequately

TABLE 6. OBSERVED AND EXPECTED FREQUENCIES OF GENOTYPIC CLASSES FOR REACTION TO RACE 57 CROWN RUST BASED ON CORRECTED F₂ DATA FOR CROSSES BETWEEN RESISTANT PARENTS HAVING NON-ALLELOMORPHIC FACTORS FOR RESISTANCE

Genotypes	Cross ^a															
	Ukraine x Victoria†		Victoria x Klein 69B†		Landhafer x Victoria†		Klein 69B x Landhafer†		Trispemia x Landhafer†		Landhafer x Santa Fe†		Klein 69B x Ukraine		Santa Fe x Klein 69B†	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
Breeding true	27	30	24	20	52	26	0	2	0	6	41	49	8	4	0	6
Female type	13	3	10	5	13	7	9	9	22	25	41	49	31	36	20	23
Male type	5	3	4	5	1	13	1	2	6	6	7	8	12	4	6	6
Susceptible																
Segregating	11	10	19	10	2	13	..	..	..	..	..	..	7	13	..	..
Parental types	6	6	9	10	20	13	..	..	..	..	..	..	9	8	..	..
Female type and susceptible																
Male type and susceptible	9	10	5	10	15	26	..	..	..	..	..	..	12	13	..	..
Female and male type and susceptible	13	21	7	20	2	7	..	..	..	..	..	..	22	24	..	..
Bulked classes	..	..	..	..	..	..	27	26	71	62	63	56	..	..	66	57
Chi-square	38.1		25.1		63.6		2.5		7.7		2.3		23.9		7.0	
Probability	<.01		<.01		<.01		.8-.9		0.02		.8-.9		<.01		.05-.1	

^aFemale parent listed first in each cross.

†Expected numbers computed according to the assumptions that Ukraine's two linked factor pairs with 23 percent crossing over were epistatic to the Victoria and Klein 69B factor pair, the Landhafer factor pair was epistatic to the Victoria, Klein 69B and Trispemia factor pair, the Santa Fe pair was epistatic to the Klein 69B factor pair, and the Victoria pair was epistatic to the Klein 69B factor pair.

‡Expected numbers computed according to the assumption of segregation for two factor pairs for resistance but parental resistant types were indistinguishable.

identify the genotypic class. The major discrepancy, as shown in table 6, was in the class segregating into parental types where an excess number was observed and in the class segregating into parental types and susceptible types where too few were observed. It is quite probable some misclassification occurred, due to small numbers involved in the progeny test.

In the segregating portion of the population the classes segregating for the Victoria type were expected to give three Victoria type to one other type. The observed numbers were 190 Victoria to 65 other where the expected were 191 to 64, showing excellent agreement. In the portion segregating for the Klein 69B type and susceptible type, too many plants were classified susceptible. This probably resulted from incomplete dominance of the Klein 69B type of resistance over susceptibility.

In the cross Landhafer x Victoria the assumption of two independent factor pairs was made. The corrected F_2 data for this cross are shown in table 6, but again the Chi-square value indicates poor agreement of the observed with the expected. Again the number of plants available for the progeny test was insufficient to correctly identify the genotypic class. Some of the greater-than-expected number observed in the class breeding



Fig. 8. Typical segregation obtained in the F_2 of crosses of resistant by resistant parents (Ukraine x Victoria) where resistance was controlled by non-allelic factors. (1) Ukraine parent, (2) recovery of Ukraine type, (3) intermediate resistant type, (4-5) recovery of the Victoria type, (6) fully susceptible, (7) Victoria parent.

true for the Landhafer type probably belong in the classes segregating for parental types and segregating for parental types and susceptible plants. The observed deficiency in the class true-breeding susceptible is difficult to explain.

Since the Landhafer type of resistance was epistatic to the Victoria type, in the segregating portion of the population it was expected that three Landhafer types to one other type (either Victoria or susceptible) would occur. The observed numbers were 265 Landhafer types to 120 other types where the expected were 289 to 96. The discrepancy here was fairly high and probably due to incomplete dominance and epistasis of the Landhafer factor in the heterozygous condition.

Typical F_2 segregation from crosses of resistant varieties having non-allelic factors for resistance is shown in fig. 8.

2. Crosses with the Landhafer factor

The Landhafer type of resistance is utilized in many breeding programs at the present time. The crosses of Landhafer with Clinton and Landhafer with Victoria were discussed previously. Results indicated that the Landhafer type of resistance is controlled by a single factor pair. The crosses of Landhafer with Ukraine and Anthony-Bond x Boone were not available for study. Crosses of Landhafer with the other resistant parents used in this study yielded susceptible progenies, indicating that resistance was controlled by non-allelomorphic factors.

In the cross Landhafer x Klein 69B the assumption was made that an independent single factor pair from each parent controlled resistance. The corrected F_2 data are shown in table 6. The Landhafer type of resistance was partially epistatic to the Klein 69B type. The total number of F_2 plants available for testing was only 37, and no true-breeding Klein 69B type lines were recovered; only one true-breeding susceptible line was recovered where two of each type were expected. The partial dominance of both types of resistance over susceptibility and the partial epistasis of the Landhafer type over the Klein 69B type made exact classification in the segregating portion of the population impossible. Therefore the segregating classes were grouped together, as in table 6, and the F_3 data are not presented.

In the cross Landhafer x Trispermia the data indicated that the parents differed by one factor from each parent. The Trispermia parent used in this cross was not from the same selection used in the cross of Trispermia x Clinton where the Trispermia parent was assumed to have three independent factor pairs for resistance. The Trispermia parent used in this cross had a very low type of resistance. Further comments on Trispermia will be found in the discussion section. The Landhafer type of resistance was epistatic to the Trispermia resistance, and the observed data are shown in table 6. A good fit was observed in all classes except

those breeding true for the *Trispermia* type of resistance. The *Trispermia* resistance was weak in the first-leaf stage and caused difficulty in separation of types breeding true for resistance and those segregating for the *Trispermia* type of resistance and susceptibility. No counts were attempted on the phenotypic types in the segregating portion of the F_3 lines.

The cross Landhafer x Santa Fe was of major interest since these two types of resistance are the ones most widely used in the present-day breeding program. Crosses of these two varieties with susceptible Clinton and resistant varieties discussed previously established that resistance of each of these two varieties was controlled by a single factor pair. The resistant reaction was a zero type in each case, and the parental types could not be separated in the segregating generations. The observed and expected data for this cross are shown in table 6, where the expected numbers were computed on the assumption of segregation for two factor pairs. Since the parental types were not distinguishable from each other, only three classes could be identified, as shown in table 6. The observed data corresponded closely with the expected.

In the segregating portion of the population a ratio of 7 resistant to 1 susceptible was expected, or from a total of 1,062 seedlings the expected numbers were 956 resistant to 106 sus-



Fig. 9. Segregation obtained in the F_2 of crosses of resistant by resistant parents (Landhafer x Santa Fe) where resistance was controlled by non-allelic factors and a higher type resistance than that exhibited by either parent was obtained. Left to right: (1) Landhafer parent, (2) immune type (higher type resistance than either parent), (3-4) recovery of parental types, (5-6) intermediate reaction, (7) fully susceptible, (8) Santa Fe parent.

ceptible where the observed were 949 to 113, which was a satisfactory agreement.

This cross yielded the best data concerning the possibility of combining two or more types of resistance to obtain a higher type of resistance. From the total of 111 F_3 lines two lines bred true for an immune type reaction. This was a higher type reaction than that exhibited by either parent. If this reaction was the result of the genotype of the double dominant factors, the expected number would have been seven lines where only two were observed. Only further crossing of these two lines will establish the genotypic constitution of this immune reaction.

The type segregation obtained in the F_2 from this cross is shown in fig. 9.

3. Crosses with Klein 69B

The three crosses remaining to be discussed all had Klein 69B as one parent. The other parents were Ukraine, Santa Fe and Trispermia. All parents were resistant to crown rust race 57, although they differed in their type of reaction.

In the cross Ukraine x Klein 69B the expected results were based on the assumption that the Ukraine factors were epistatic to the Klein 69B factor. The expected numbers according to the assumption are presented with the observed numbers in table 6. While the Chi-square value indicates an unsatisfactory fit, the genetic pattern seems to agree with other information already discussed.

In the segregating portion of the population the ratio in the class segregating into parental types was expected to be 83.2 percent Ukraine type to 16.8 percent Klein 69B type. The expected numbers were 57 to 11 and the observed were 54 to 15. In the portion segregating for parental types and susceptibility, the expected ratio was 81.7 percent Ukraine type, 13.8 percent Klein 69B type, 4.6 percent susceptible. The expected numbers were 322 to 54 to 18 while the observed were 275 to 55 to 64. In the class segregating for Klein 69B and susceptible types where the expected was a 3 to 1 ratio, the observed numbers were 71 Klein 69B to 109 susceptible. Again the Klein 69B factor in the heterozygous condition led to misclassification.

In the cross Santa Fe x Klein 69B the assumption was made of segregating for two independent factor pairs. The Santa Fe type resistance was epistatic to the Klein 69B type of resistance. The expected and observed data are shown in table 6. The observed agree well with the expected except in the recovery of the true-breeding Klein 69B type. The resistance of Klein 69B always was difficult to identify in the segregating groups, and it was particularly difficult to separate those breeding true for the Klein 69B type from those segregating for the Klein 69B type and susceptibility.

In the cross Klein 69B x *Trispermia*, both parents had a very weak type of resistance. Fully susceptible plants were obtained in the F_2 and the F_3 , but the difficulties involved in classification were such that the data were not sufficiently reliable to satisfy a genetic interpretation. Complete gradations from a weak type of resistance to fully susceptible plants made it impossible to group individual plants consistently into one class or another. The occurrence of resistant types and fully susceptible types could be identified, however.

DISCUSSION

A summary of the proposed genotypes of the varieties investigated is presented in table 7. Below table 7 are given the various allelic and non-allelic relationships of the proposed genotypes. It is realized that in some cases the data were not extensive nor complete enough from any one cross to identify the genotypes of the parental varieties. However, each cross provided critical information on other crosses. Any hypothesis that could explain the results of all crosses was probably correct even though an unsatisfactory fit may have been indicated by the Chi-square test for an individual cross. The breeding behavior of several varieties in diallel crosses should provide a critical test of genetic hypotheses even where the amount of data for any one cross is small and subject to large chance deviations.

This study was designed with the assumption that the parental varieties were genotypically homogenous for their particular type of crown rust reaction. The results of this study indicated that this assumption was not valid. The origin of many of the parental varieties was not definitely known. It is quite reasonable to assume that the parents used in this study were not descendent from a single homozygous plant. Therefore, even if selection for crown rust reaction type had been practiced, it seems unlikely that all plants would be of the same genotype since these data indicate the presence of duplicate or triplicate factors in some of the varieties.

TABLE 7. PROPOSED GENOTYPE OF PARENTAL VARIETIES USED IN THE INVESTIGATION OF INHERITANCE OF RESISTANCE AND SUSCEPTIBILITY TO CROWN RUST RACE 57.*

Landhafer	LL	mm	vv	uu	kk	ikik
Santa Fe†	ll	M ₁ M ₁	vv	uu	kk	ikik
Victoria	ll	mm	VV	uu	kk	ikik
Ukraine	ll	MM	vv	UU	kk	ikik
Klein 69B	ll	mm	vv	uu	KK	ikik
<i>Trispermia</i> ‡	ll	M ₂ M ₂	..	..	kk	ikik
Anthony-Bond x Boone§	ll	M ₂ M ₂	V ₁ V ₁	..	kk	ikik
Clinton	ll	mm	vv	uu	kk	IkIk

*The M loci and the U loci are linked with 22.88 ± 0.04 percent crossing over.

†Santa Fe may in some cases carry alleles to both M and U.

‡*Trispermia* may carry one, two or three factors for resistance, but the allelic relationship has only been established for one factor.

§Anthony-Bond x Boone may carry one, two or three factors for resistance, but allelic relationships have been established for only two factors.

The rust reaction of Klein 69B was uniform for all parents, but the reaction to the race of the rust fungus used in this study was difficult to classify in the progeny lines and added to the discrepancies observed in the assignment of lines to genotypic classes. The adult plant reaction of Klein 69B was different from the seedling reaction. In the field Klein 69B gave a very high type (zero) reaction with race 57 under epiphytotic conditions.

The rust reaction of the parental plants of the variety *Trispermia* varied considerably. Crosses with parental plants showing the highest type resistance indicated that more factor pairs were involved than in the lower type of resistance in other parental plants. The variety *Trispermia* was heterogenous for genetic factors involved in resistance to crown rust race 57. As explained in table 7, plants of the variety *Trispermia* may have any combination of the three factor pairs. Each additional factor pair adds to the degree of resistance. As was the case for Klein 69B, the adult plant reaction under an epiphytotic of race 57 showed a higher type resistance than did the seedling. Variation was still present among the parental plants within the variety in adult plant reaction and corresponded with the variation described for the seedling plants.

The reaction of various parental plants from the variety *Victoria* was uniform and characteristic of this variety. The *Victoria* type reaction varied a great deal in F_3 lines homozygous for the *Victoria* factor pair. Whether this variation among lines derived from *Victoria* crosses and homozygous for the *Victoria* factor was due to background effect or minor factors was not determined.

Since the *Victoria* type of crown rust reaction is distinct from the other types, it is interesting to speculate on why it differs. The theory of ultra-susceptibility—that because the *Victoria* type is so susceptible, the pathogen kills the host cells so rapidly that little or no sporulation occurs, and thus the host is resistant—has been proposed by several investigators. Litzenberger (6, pp. 476-477) in a study of crosses of *Mindo* x *Victoria* to determine the inheritance of reaction to race 1 of crown rust stated:

"Factorial analysis presented in Table 6 assumes that A and B are complementary and V is expressed only when in presence of germ plasm susceptible to *P. coronata avenae*. That is, when A and B are present to give the Bond type of resistance the fungus is prevented from developing to the sporulation stage, when tissue collapse (conditioned by V) normally begins."

The data obtained in this study support his conclusion that the *Victoria* type reaction is not expressed in the presence of other factors giving an immune or zero type reaction, but the conclusion that V is expressed only in susceptible germ plasm is not in agreement with results of this investigation. In crosses of *Victoria* with resistant parents Klein 69B and Anthony-Bond

TABLE 8. ESTIMATION OF LINKAGE INTENSITY OF DUPLICATE GENES, CONTROLLING RESISTANCE TO CROWN RUST RACE 57, IN THE VARIETY UKRAINE FROM F₂ DATA CORRECTED BY F₃ PROGENY TEST.

Cross	Bred-true Ukraine type	Segregated parental types	Bred-true other parent type	Total	Maximum likelihood estimation of recom- bination
Ukraine x Trispermia	44	60	12	116	
Santa Fe	52	70	26	148	
A.-B. x Boone	17	36	10	63	
Clinton	50	67	21	138	
Total	163	233	69	465	22.88±.04

x Boone the Victoria type reaction was expressed in resistant germ plasm. There is no way to determine whether the Victoria gene conditions a resistant or a hyper-susceptible reaction (resulting in a resistant classification). Either way it is intermediate on the scale of dominance or epistasis in relation to other genes for crown rust resistance to race 57.

The variety Santa Fe also varied in its genotype for crown rust resistance. This study indicated that plants of the variety Santa Fe may carry one or both of the factor pairs allelic to the Ukraine linked duplicate factors. Santa Fe often shows some pustule formation, sometimes as much as a 2 type reaction. The basis for variation, environmental or genetic, has not been shown.

The variety Ukraine was assumed to have a genotype of two duplicate linked factor pairs controlling resistance to crown rust race 57. A crossover value of 23 percent was estimated from the cross of Ukraine x Clinton. A better estimation of linkage intensity may be made by use of data from other crosses with Ukraine. A summary of the data used and the estimation of percent crossing over with its standard error are given in table 8. While all the Ukraine parents used in this study had the same genotype for crown rust resistance, it should be quite possible to find plants in the variety Ukraine with only one of the two factor pairs.

The reaction of the variety Landhafer was consistent and involved only one factor pair. The degree of dominance of this factor was not as high as that of some others.

All data from crosses involving Clinton indicated that this variety carried only the recessive alleles to factors for resistance except in the case of Clinton x Klein 69B. In that cross the data indicated that Clinton carried a dominant inhibitor factor pair which was epistatic to the Klein 69B factor pair for resistance.

The data on the Anthony-Bond x Boone parents indicated that

their genotypes probably were the same. However, in this selection it could be expected to find plants having different genotypes for resistance to crown rust.

The data from this study indicated that at least eight genes at five loci were involved in determining resistance to one race of the crown rust organism. Even with only five loci (more are known and probably many more exist) 31 combinations of one or more of these genes at separate loci in the homozygous condition could be obtained. The number of possible factor combinations at these five loci is much greater since alleles exist for certain loci. It would be desirable to have available all of these combinations, but the mechanics of their isolation, for even one race of the crown rust fungus, are so difficult that this objective may never become a reality. The solution of the problem then becomes limited by practicability. The rust problem may never be completely solved by breeding, due to changes in races, but probably the total genetic variation of oats is equally as great and the utilization of this germ plasm in a breeding program can prevent serious losses due to rust.

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